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Boletus vigasensis sp. nov. an edible species from coniferous forests of Veracruz, Mexico

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Abstract—A new *Boletus* species belonging to the Aereus group was found among specimens collected in coniferous forest in the Cofre de Perote Mountain area in central Veracruz State; and also among specimens obtained in a local traditional market in the city of Xalapa, Veracruz, where such fungi are sold and used by the locals and offered in restaurants. Morphological and molecular analyses of the species are presented, accompanied with photographs and line drawings.

Key words—American boletes, ectomycorrhizal mushrooms, wild edible mushrooms, porcini mushrooms

Introduction

There are currently around 2486 names of species identified within *Boletus*, but due to molecular systematics research made in the last decade, this number has been reduced to about 1245, corresponding to around 800 accepted species distributed worldwide (http://www.indexfungorum.org). Over time, various lineages (sections) in the genus have been recognized, and based on the application of molecular studies, *Boletus* sect. *Boletus* (the "porcini" clade s.str.) together with five lineages (Aereus, Alloboletus, Inferiboletus, Obtextiporus, and Variipes; not yet formally described) are currently accepted (Dentinger & al. 2010, Feng & al. 2012, Nuhn & al. 2013, Cui & al. 2016).

It is well known that the edible bolete species around *Boletus edulis* Bull. have been collected and consumed since ancient times (Hall & al. 1998, Leonardi & al. 2005, Sorrenti 2017), being among the most collected edible wild mushrooms and considered a culinary delicacy with significant commercial demand worldwide (Singer 1986, Boa 2004, Arora 2008, Sitta & Davoli 2012). Species related to *B. edulis* are found to a wide extent throughout the Northern Hemisphere (Lakhanpal & al. 1988, Yamanaka & al. 2000, Nounsi & al. 2014, Outcoumit & al. 2014, Bozok & al. 2020), and some of them have been introduced in New Zealand and South Africa (Wang & al. 1995, Hall & al. 1998). Additionally, *B. albobrunnescens* Desjardin & al. has recently been recognized as endemic to Thailand and *B. austroedulis* Halling & N.A. Fechner as endemic to Australia (Halling & al. 2014).

Wild mushroom species morphologically resembling European *B. edulis* have been consumed in Mexico since pre-Hispanic times. These are recognized in Spanish terms as "panzas", "pancitas", "cemitas", etc., and in various names in native languages, for example "sekub t´ul" (Tsotsil), "serochaco", "sonaka" (Raramuri), "jopante", "Jthä", (Otomí), "baya retni", "mey guiet xtil" (Zapotec), "pante", "xotoma", "xotomate", "pananácatl" (Náhuatl), among others (Herrera & Guzmán 1961, Guzmán 1997, Jarvis & al. 2004, Garibay-Orijel & al. 2009, Lara & al. 2013, Quiñónez-Martínez & al. 2014, Ruan-Soto 2018, Jaime 2019, Montoya-Esquivel & al. 2003, 2019). In the region of Xalapa, Veracruz, and possibly in other areas of Mexico, due to foreign influence, the name "porcini" began to be part of the language among merchants and has spread gradually in traditional markets by the local vendors. It is evident that the culinary use of that group of mushrooms in urban areas of the country has a notable increase following the trends of international cuisine.

Mexico is diverse in terrestrial ecosystems, and edible species of *Boletus* are collected in many regions, but there is special emphasis on this activity in the central zone, along the Trans-Mexican Volcanic Belt (Herrera & Guzmán 1961, Mapes & al. 1981, Bandala & al. 1997, Montoya-Esquivel & al. 2003). In this vast mountain range are the highest peaks of the country, including important forest areas such as the Cofre de Perote National Park, which includes an extinct volcano (Cofre de Perote or Nauhcampatépetl [its Náhuatl name]) that reaches 4282 m in altitude. This area is located 64 km away from the city of Xalapa (Veracruz state capital) and is where our collections of *Boletus* specimens were made. This mountain hosts coniferous forests and oak-conifer forests that favor

the development not only of *Boletus* species but also of other edible fungi. At the site, an important folk knowledge about the use of around 53 edible species of mushrooms is culturally conserved; such fungi are harvested and form part of the "basic family basket of edible natural products", and even represent a source of income for the locals (Bandala & al. 1997).

The taxonomy and classification of the species in the *Boletus edulis* group, mainly due to their economic importance in different regions of the world, is gradually being revised (Dentinger & al. 2010, Feng & al. 2012, Halling & al. 2014, Cui & al. 2016, Gelardi 2020) to the point that mycelium of the species is being certified, with morphological and molecular support, for long-term reforestation programs that increase the production of sporocarps (Mello 2012). Despite the widespread use of sporocarps of *B. edulis* group and even of other edible fungi in Mexico, little taxonomic research has been conducted to estimate their specific diversity in the country. Most records have often focused on some macroscopic characters, such as size, form, taste, and color. We have approached the taxonomic revisions of apparently well-defined Mexican macrofungi species, which have been commonly cited under names of European or American (USA) species but which in fact, correspond to other taxa. Obviously, such broad concepts underestimate the diversity of Mexican species. Furthermore, to generate suitable protocols for their commercial sale, we consider the identification of wild edible mushrooms as a basic task, which would help to position specific taxa within the global market, trace their natural and commercial distribution, facilitate the allocation of prices, and guarantee hygiene and food safety. In addition, proper identification will help to protect their populations. In this work, we review the status of collections from the Cofre de Perote Mountain superficially similar to *B. edulis*, a site where their fruiting and harvesting are common. Fruit bodies purchased from local markets, where they are popularly traded, were also included — they come from this mountain, according to the traders. A morphological study together with molecular evidence implies the existence of more than one species, but here we focus just on the one for which we had best support for recognition as a new species. It presents all the characters defining *Boletus* and, in our phylogeny (Fig. 1), it is distant from the *B. edulis* clade, but related to the Aereus group. This species is proposed here as a new species, *Boletus vigasensis*, which is described, illustrated, and taxonomically discussed.

Materials and methods

Sampling and morphological study

Basidiomes of specimens of *Boletus* superficially resembling those of "porcini" fungi were collected during 2015 and 2018 in the Natural Protected Area "San Juan del Monte", located in the municipality of Las Vigas, on the Cofre de Perote Mountain, in Veracruz State (Eastern Mexico), of the Trans-Mexican Volcanic Belt, at an altitude of 2520–2770 m, in mixed pine forests of *Pinus patula* Schltdl. & Cham., *P. pseudostrobus* Lindl., and *P. teocote* Cham. & Schltdl. The climate varies from cold subhumid to mild subhumid, with annual average temperatures between 12–18°C, and 1000–1800 mm average annual rainfalls. In the city of Xalapa, 64 km east of Cofre de Perote, we also bought some fruitbodies at the Alcalde y García traditional market which were harvested on that mountain.

Descriptions of colors, macromorphological, and organoleptic characteristics were gathered from fresh samples; color records follow Munsell (1994; e.g., 2.5Y8/3) and Kornerup & Wanscher (1967; e.g., 5B5). The preservation, micromorphological study, and the line drawings were developed according to Montoya & al. (2019). In the descriptions, Xm denotes the mean values of length and width of basidiospores per collection in n collections and its standard deviation, and Qm refers to the range of coef. Q (where Q is the average of the ratio length/width of basidiospores in each collection). Collections are deposited in the Herbarium of Instituto de Ecología A.C., Xalapa, Veracruz, México (XAL).

DNA extraction, PCR and sequencing

DNA extraction was performed according to César & al. (2018). Following previous research on the genus *Boletus* (Leonardi & al. 2005, Dentinger & al. 2010, Cui & al. 2016, Wu & al. 2016, Chakraborty & al. 2017, Sarwar & al. 2018, Tremble & al. 2020), the internal transcribed spacer (ITS) region of ribosomal DNA was extracted and amplified according to previous protocols, using the primers ITS1F, ITS5/ITS4 (White & al. 1990, Gardes & Bruns 1993). Sequencing of the amplified PCR products was performed on a Genetic Analyzer 3730XL sequencer (Applied Biosystems). All the sequences obtained were edited, assembled, and deposited in the GenBank database (Benson & al. 2017). Accession numbers are indicated in Fig. 1.

Phylogenetic analysis

With the sequences obtained, we developed a similarity analysis from GenBank, using the BLAST program. The sequences produced in this work (Fig. 1) together with all the ITS sequences available in the GenBank (GB) database named as *Boletus* (1078 sequences), were used to build a data set using the PhyDE v.0.9971 program (Müller & al. 2010). The alignment was carried out with the MAFFT online service program (Katoh & al. 2019), and the inconsistencies were corrected manually. The phylogenetic tree was generated (data not shown here), and the evolutionary model was calculated using the IQTree v2.1.1 package (Nguyen & al. 2015, Kalyaanamoorthy & al. 2017, Minh & al. 2020), and the best-fit model, using the Bayesian Information Criterion

(BIC), the Akaike Information Criterion (AIC), and corrected AIC. The latter was used to generate a phylogenetic tree with the Maximum Likelihood (ML) method, with a Nearest Neighbour Interchange (NNI) heuristic, with a specific evolutionary model for data set. By default, the IQTree program generated a consensus tree by calculating the Robinson-Foulds distance between the ML tree and the consensus tree, with the branches being tested by means of Ultrafast Approach Bootstrap (UFBoot), SH-like approximate Likelihood Ratio Test (SH-aLRT), Approximate Bayes test (aBayes) and Bootstrap Standard (BS). After a second optimized alignment of the entire genus *Boletus*, an inferred phylogenetic tree with high molecular support was generated being consistent and the same clades are presented in the tree of Fig. 1. Another phylogenetic tree was generated also by Bayesian Inference (BI), using MrBayes v. 3.2.7 (Ronquist & al. 2012). The phylogenies from ML and BI analyses were displayed using FigTree v1.4.4 (Rambaut 2018). Being consistent with both phylogenetic trees (ML phylogenetic tree and BI phylogenetic tree), the Bayesian posterior probability values are presented in the branches of Fig. 1.

Results

In the phylogeny obtained, the sequences of the two new Mexican specimens formed an independent and strongly supported clade. Macromorphological features such as pileus and tube color, and white to staining pale brown to lilaceous context, combined with micromorphological features such as size of basidiospores and cystidia, and a well differentiated ixotrichoderm are distinctive taxonomically from close relatives to consider that the samples represent a new species. In the phylogeny obtained it appears related to *B. occidentalis* B. Ortiz & T.J. Baroni described from Dominican Republic, *B. atkinsonii* Peck from USA, and *B. barrowsii* Thiers & A.H. Smith from USA and Mexico.

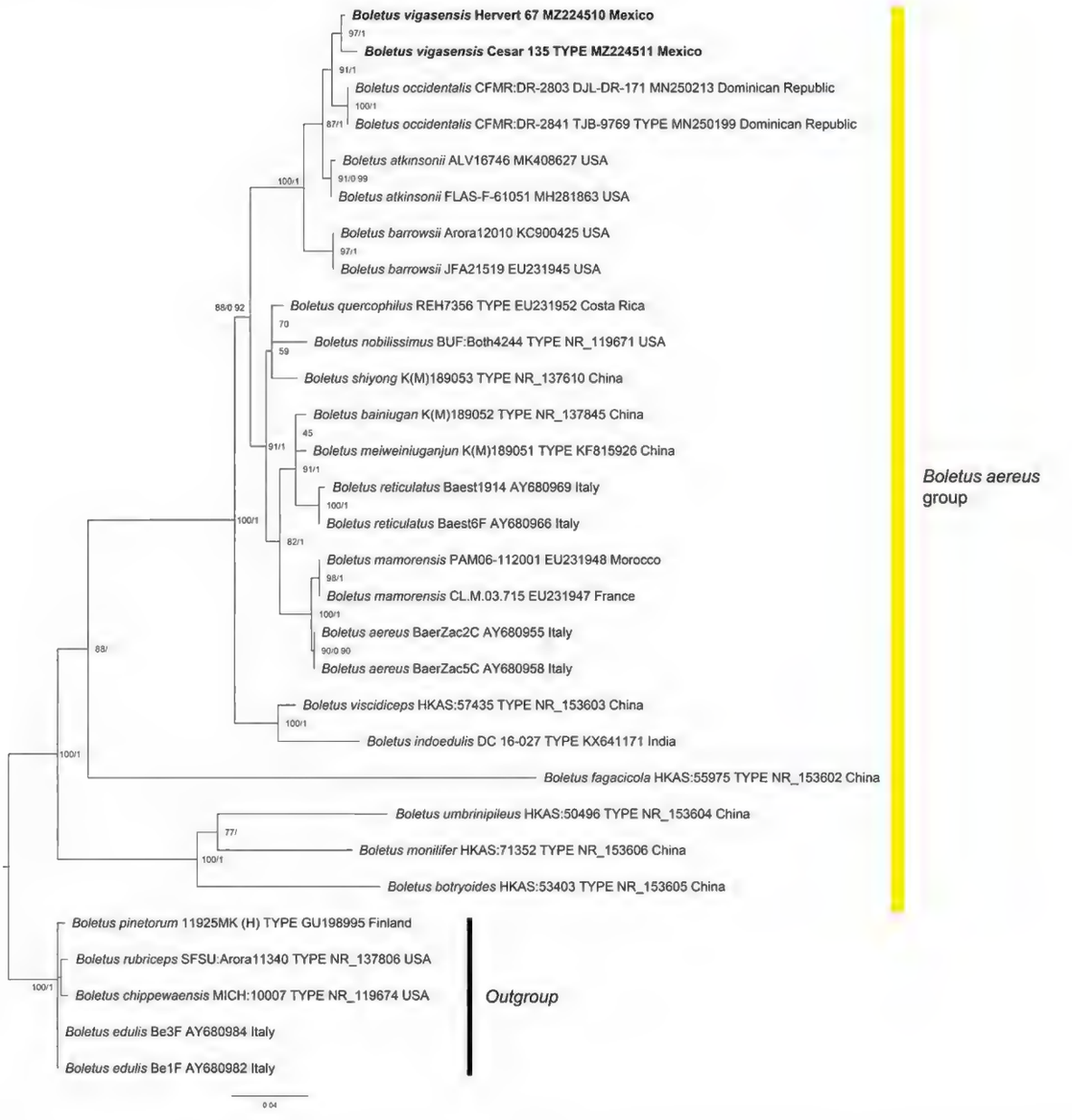
Boletus vigasensis Hervert 67 MZ224510 Mexico
Boletus vigasensis Cesar 135 TYPE MZ224511 Mexico
Boletus occidentalis CFMR:DR-2803 DJL-DR-171 MN250213 Dominican Republic
Boletus occidentalis CFMR:DR-2841 TJB-9769 TYPE MN250199 Dominican Republic
Boletus atkinsonii ALV16746 MK408627 USA
Boletus atkinsonii FLAS-F-61051 MH281863 USA
Boletus barrowsii Arora12010 KC900425 USA
Boletus barrowsii JFA21519 EU231945 USA
Boletus quercophilus REH7356 TYPE EU231952 Costa Rica
Boletus nobilissimus BUF:Both4244 TYPE NR_119671 USA
Boletus shiyong K(M)189053 TYPE NR_137610 China
Boletus bainiugan K(M)189052 TYPE NR_137845 China
Boletus meiweiniuganjun K(M)189051 TYPE KF815926 China
Boletus reticulatus Baest1914 AY680969 Italy
Boletus reticulatus Baest6F AY680966 Italy
Boletus mamorensis PAM06-112001 EU231948 Morocco
Boletus mamorensis CL.M.03.715 EU231947 France
Boletus aereus BaerZac2C AY680955 Italy
Boletus aereus BaerZac5C AY680958 Italy
Boletus viscidiceps HKAS:57435 TYPE NR_153603 China
Boletus indoedulis DC 16-027 TYPE KX641171 India
Boletus fagacicola HKAS:55975 TYPE NR_153602 China
Boletus umbrinipileus HKAS:50496 TYPE NR_153604 China
Boletus monilifer HKAS:71352 TYPE NR_153606 China
Boletus botryoides HKAS:53403 TYPE NR_153605 China
Boletus pinetorum 11925MK (H) TYPE GU198995 Finland
Boletus rubriceps SFSU:Arora11340 TYPE NR_137806 USA
Boletus chippewaensis MICH:10007 TYPE NR_119674 USA
Boletus edulis Be3F AY680984 Italy
Boletus edulis Be1F AY680982 Italy
Boletus aereus group
Outgroup

FIGURE 1. Phylogenetic relationships within *Boletus* species inferred from the ITS sequences by maximum likelihood method. The new species is indicated in bold letters. Bootstrap scores ≥70% and Bayesian Posterior Probabilities ≥0.90 are indicated above the branches.

Taxonomy

Boletus vigasensis Montoya, E. César, Ant. Ramos & Bandala **sp. nov.** FIGS 2–4

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Differs from other *Boletus* spp. by its pale brownish to greyish-orange pileus, its context white staining brown to violaceous, its mustard-brown to orange-brown pores, its basidiospores 13–16.5(–19.5) × 4.5–5 µm, its long pleurocystidia, and its pileipellis as a slightly gelatinized trichoderm.

Type. —Mexico, Veracruz, Cofre de Perote mountain, Municipality of Las Vigas, San Juan del Monte, 19.6147°N 97.1117°W, 2528 m.a.s.l., solitary near *Pinus pseudostrobus* in a mixed pine forest with *Pinus patula* and *P. teocote*, 29 August 2018, César 135 (Holotype, XAL; GenBank ITS MZ224511; 28S MZ198357; rpb1 MZ233731).

Etymology—The epithet refers to Las Vigas, the town closest to the San Juan del Monte protected natural area.

Pileus 41–116 mm diam., subhemispheric, convex to plano-convex when mature, surface regular, sometimes slightly cracked, somewhat punctate pruinose, soft, at times with detachable cuticle, surface pale brown (2.5Y 7/4), pale greyish-orange (10YR 5/4-4/4; 6D5), pale brown (10YR 4/6; 5D7, 5D5), below pileus cuticle pale pinkish-brown (7.5YR7/2; 6B2); when young with incurved margin, straight or undulate when mature. Hymenophore plane to slightly convex. Tubes 18–35 mm in length, straight, adnate, greyish (2.5Y 7/2, 7/3; 4B2) when young, changing to pale mustard-yellow (2.5Y7/6; 4B5), unchanging when bruised. Pores <1 mm diam, round to slightly angular, pale mustard-brown (2.5Y6/8; 4B7) to cinnamon-brown or faintly orange (10YR5/6, 6C6), when bruised dark brown (10YR3/1; 6F4), with a whitish layer of tangled hyphae covering the pores (stuffed pores) at primordia or in immature specimens. Stipe 70–121 × 31–49 mm, clavate to subclaviform, straight or curved, attenuated towards the pileus attachment, broadened towards the base; compact, dull, fibrillose, with a fine and moderately open mesh from the top to the middle of the stipe, which appears pale greyish-beige (2.5Y6/4) to chocolate-brown (10YR 4/4), in the primordia the apex is dark greyish-beige (2.5Y5/4; 5C4) to pale beige (2.5Y 6/4–7/4), with a white base. Context 9–20 mm broad, whitish, compact, staining pale brown (10YR 7/3; 5B3) to vinaceous-lilaceous (7.5YR6/3; 7C3) especially towards the cuticle. Odor fungoid, mild, somewhat similar to steam cooked vegetables. Taste mild, fungoid, agreeable.

Macrochemical test: pileus surface slightly reddish to violaceous with NH_4OH vapors.

Figure 2. *Boletus vigasensis*: basidiomes: a. XAL–César 135 (holotype); b. XAL–Hervert 67. Scale bars: a = 20 mm; b = 10 mm.

Basiospores 13–16.5(–19.5) × 4.5–5 µm, Xm = 14.86 ± 1.50 × 4.56 ± 0.17, Qm = 3.25 ± 0.31, fusiform to narrowly ellipsoid, with slight suprahilar depression, pale yellowish, smooth; wall up to 0.5 µm thick. Basidia 25–37(–41) × 9–13 µm, commonly tetrasporic, at times tri- and bisporic, thin walled, hyaline. Pleurocystidia 46–62 × 7–13 µm, narrowly lageniform, hyaline, thin

walled, infrequent. Cheilocystidia 24–47 × 5–10 µm, like pleurocystidia, some narrowly subutriform or apically tortuous other clavate, hyaline, at times pale yellowish, thin walled, infrequent. Caulocystidia 27–62 × 6–10 µm, narrowly lageniform or broadly lageniform some subcylindrical, often somewhat tortuous, hyaline, thin walled, at times thick-walled (c. 1 µm thick). Pileipellis a slightly gelatinized trichoderm, formed by elements disposed in chains, mostly grouped in cumulus, intercalary elements 4–10 µm diam, pale yellow, hyaline, thin-walled, some collapsing; terminal elements 17–62 × 6–10(–13) µm, lageniform, subfusiform, lecythiform or at times subcylindrical, thin walled, hyaline. Clamp connections absent.

Ecology & Distribution— In coniferous forest, on soil, growing under *Pinus pseudostrobus* in a mixed pine forest with *P. patula* and *P. teocote.*

Additional specimen examined—**MEXICO, Veracruz, Xalapa**, Alcalde y García market, 12 November 2015, Hervert 67 (XAL).

Comments—In the phylogeny (Fig. 1) *Boletus vigasensis* appears showing relationship among the species of the Aereus group, sister to *B. occidentalis*, which differs by its dark brown pileus when young becoming yellow brown, the unstaining white context, pores soon yellow green to olivaceous with age, the stipe with a coarse white to pale tan reticulum at the top, shorter basidiospores (11.2–15.2 × 4–4.8 µm), shorter pleurocystidia (37.6–48 × 4.8–8 µm), and pileipellis having a subgelatinous tangled layer of repent to suberect hyphae (Ortiz-Santana & al. 2007). *Boletus atkinsonii* and *B. barrowsii* are also closely related to *B. vigasensis* (Fig. 1). However, according to the protologue (Peck 1905) *B. atkinsonii* has paler (yellow or subochraceous) pores, brownish stipe reticulum and shorter basidiospores (10–12.7 × 4–5 µm, Peck 1905; 10–14 × 3.5–4.5 µm, Smith & Thiers 1971). Basidiomes of *B. barrowsii*, according to the protologue (Thiers 1976) reach a bigger size, with the pileus up to 300 mm and with "pale pinkish buff" to "pinkish buff" colors during all stages of development, the tubes shorter (10–20 mm long) with wider pores (1–2 mm width), the stipe bulbous (bulb up to 90 mm broad over the base) with a typically fine and delicate reticulum often all the way to the base, unstaining context, basidiospores shorter (13–15 × 4–5 µm), cystidia shorter (37–50 × 5–9 µm), and the pileus cuticle disposed in a poorly differentiated cutis. In *B. vigasensis* the pileipellis is a well differentiated ixotrichoderm, corresponding to the type 3 proposed by Cui & al. (2016), and with a context that turns to pale brown or vinaceous-lilaceous when exposed. Other species belonging to group Aereus are *B. bainiugan* Dentinger from China, with a pileipellis in a trichoderm but without a gelatinous matrix and with frequently branched

elements; and *B. quercophilus* Halling & G.M. Muell. from Costa Rica, with yellow colored pileus, subtomentose to scaly-fibrillose at margin, and with shorter basidiospores (Dentinger & Suz 2014, Halling & Mueller 1999).

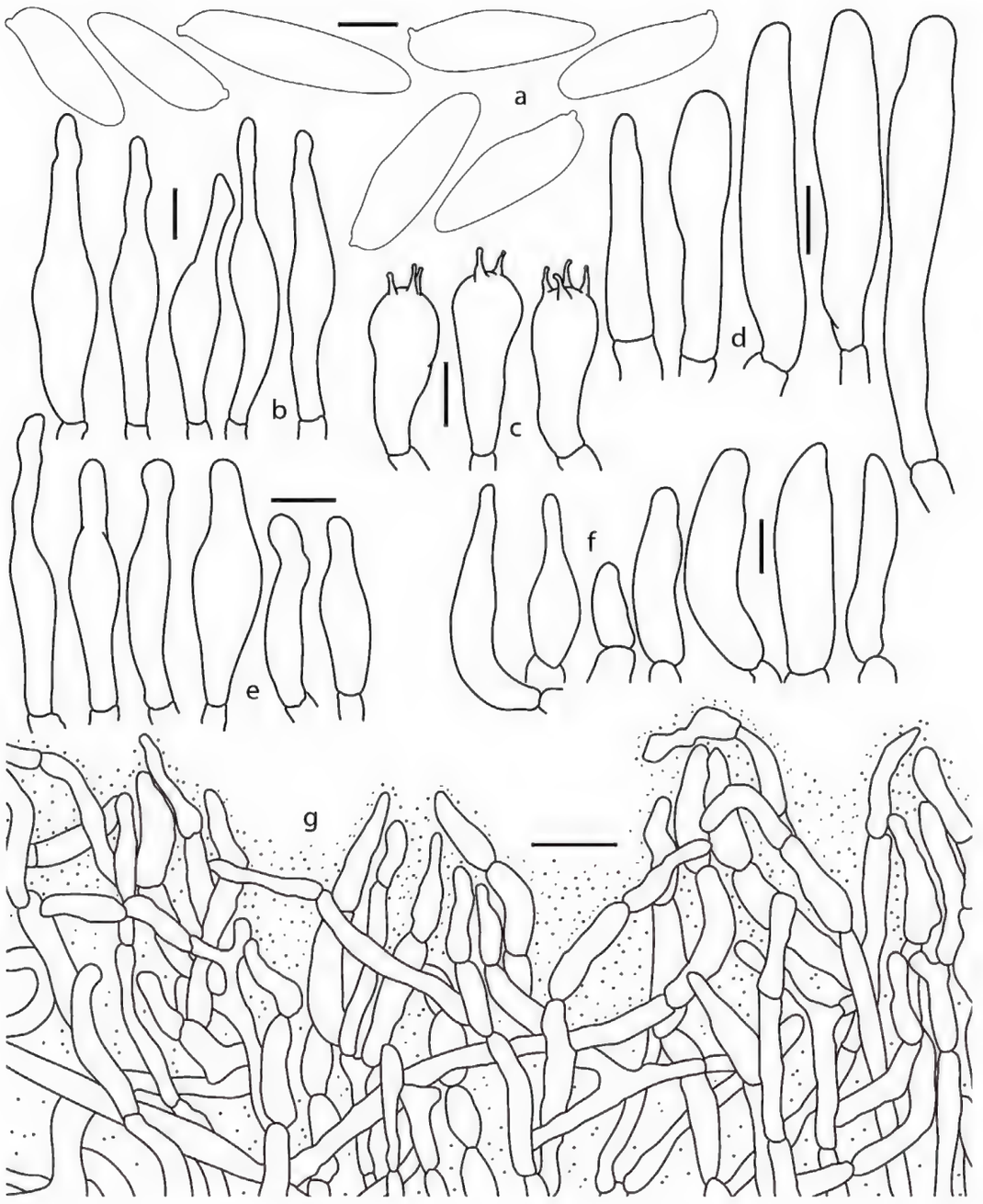

FIGURE 3. *Boletus vigasensis* (holotype, XAL–César 135): a. basidiospores; b. pleurocystidia; c. basidia; d. caulocystidia; e. cheilocystidia; f. pileipellis terminal elements; g. pileipellis. Scale bars: a = 5 µm; b–f = 10 µm.

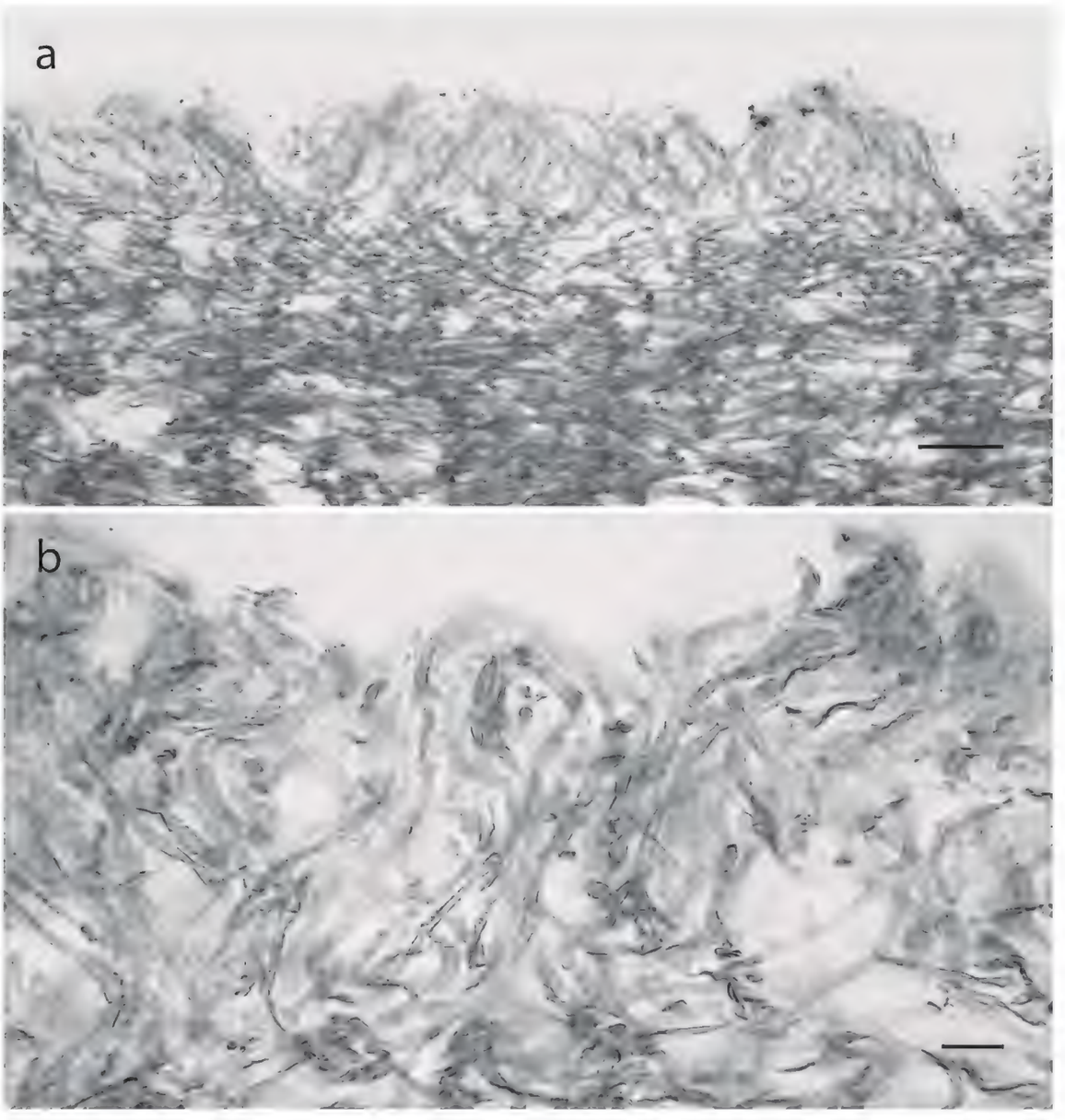

FIGURE 4. *Boletus vigasensis* (holotype, XAL–César 135): pileipellis. Scale bars: a = 100 µm; b = 25 µm.

Key to *Boletus vigasensis* and species of the Aereus group and *B.* sect. *Boletus*

(The Aereus group spp. are phylogenetically close to *B. vigasensis*; and the *B.* sect. *Boletus* spp. are morphologically similar to *B. vigasensis*)

1. Pileus developing ferruginous to vinaceous-tawny tinges 2
1. Pileus color not as above 4
2. Pores staining reddish-brown when bruised, with conspicuous hymenial cystidia 3
2. Pores and context above tubes unstaining when bruised but may show slight bluing if old or wet; hymenial cystidia inconspicuous ..... *B. rubriceps*

3. Pileus pale lemon yellow and decorated irregularly with ferruginous or vinaceous tawny spots; Pores yellowish to pale orange-brown, staining pinkish or vinaceous cinnamon on bruising; Basidiospores up to 16 µm in length, pileus context stains dingy tan ..... *B. chippewaensis*
3. Pileus with brown coloration, lacking lemon yellow hues and not irregularly marked with vinaceous spots; pores white when young, coloring with age greenish yellow, not or slightly darkening on bruising; basidiospores up to 19 µm in length ..... *B. edulis*
4. Pileus white to whitish or buff during all stages of development ..... *B. barrowsii*
4. Pileus pale brown, grayish brown to yellowish brown, even dark brown 5
5. Pileus dark brown in button stages, becoming paler with expansion .. *B. occidentalis*
5. Not as above 6
6. Context white, pileipellis hyphae roughened; basidiospores up to 14 µm in length ..... *B. atkinsonii*
6. Context staining, at least under pileus cuticle 7
7. Context yellowish under the cuticle; pores concolorous with tubes, in yellow to greenish or greyish-yellow colours; pileipellis hyphae brown, some very dark ..... *B. pinetorum*
7. Context staining pale brown to vinaceous-lilaceous especially towards the cuticle; pores pale mustard to cinnamon-brown or faintly orange, when bruised dark brown; pileipellis hyphae not as above ..... *B. vigasensis*

Discussion

Among the fungi commercialized as the porcini in Xalapa, Veracruz, solely because of the appearance of a robust and relatively large fungus, *B. vigasensis* appears related to *B. edulis*, with which in fact it has some resemblance. *Boletus edulis* is a European fungus, which in the diagnosis (Bulliard 1782) was described as edible, with pileus 250–280 mm diam (10–11 inches diam), with a firm, white, unchanging context, with white tubes when young, coloring with age, with an agreeable odor and taste. Later, the sanctioning work (Fries 1821) defined it with a pulvinate, glabrous pileus; with semi free, roundish, white but soon yellowish tubes, stipe thick and reticulate. These features, however, are not unique to *B. edulis*, but to a greater or lesser degree shared with different similar species of the "edulis complex". It is likely that derived from the popular culinary value and perhaps also from the currently significant commercial value of this mushroom, the name "*B. edulis*" has been used in different regions of the world for wild populations of fungi that at first glance are superficially similar but are taxonomically different; such is the case of *B. vigasensis*, which belongs to the Aereus group, distant from the "species complex" of *B. edulis* (*B.* sect. *Boletus*). This situation has been common to other popular highly

appreciated wild edible mushrooms (Alessio 1985, Mueller 1991, Wang & al. 1995, Guzmán & Ramírez 2001, Pilz & al. 2003, Foltz & al. 2013, Arora & Frank 2014, Huang & al. 2021).

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